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Different Susceptibilities to Low Temperature Photoinhibition in the Photosynthetic Apparatus Among three Cultivars of Cucumber (*Cucumis sativus* L.)

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Susceptibility to low temperature photoinhibition in photosynthetic apparatus was compared among three cucumber cultivars, Gahachungjang (GH), Banbaekjijeo (BB) and Gaeryangsymji (GR). By chilling in the light for 6 h, a sustained decrease in the potential quantum yield (Fv/Fm) and the oxidizable P700 contents was observed, and the decrease was less in GH than in BB and GR. Although the difference was small, some Φ_{PSII} remained in GH after light-chilling for 6 h indicating that a few electrons can flow around photosystem II (PSII). As a consequence, the primary electron acceptor of PSII, Q_A, was reduced slowly and was not fully reduced after light-chilling for 6 h in GH. Although the amplitude was small, the development of NPQ was also faster in GH, indicating a higher capacity for non-photochemical energy dissipation. The relative fraction of a fast relaxing component of NPQ (qf) was higher in GH. After light-chilling for 5 h, the values of qf in BB and GR became much smaller than that in GH, indicating BB and GR suffered more significant uncoupling of ATPase and/or irreversible damages in PSII. When fluorescence induction transients were recorded after chilling, significant differences in quenching coefficients (qQ and qN) were observed among the three cultivars.

key words: chilling, chlorophyll fluorescence, cucumber cultivars, photoinhibition, photosynthesis

INTRODUCTION

Light is an essential requirement for photosynthesis, but it is also harmful to the photosynthetic apparatus when illumination is excessive. The decrease in photosynthetic activity induced by strong light is described as photoinhibition [1]. Environmental stresses such as chilling and drought may promote photoinhibition even when illumination is moderate.

Chilling-sensitive plants, including cucumber and maize, have been used extensively for the investigation of the lesion sites of photoinhibition. The main target for photoinhibition has been generally known photosystem II (PSII) [1]. It has been suggested that there are at least two potential mechanisms for photoinhibition. Firstly, for acceptor-side photoinhibition, over-reduction of the primary plastoquinone acceptor of PSII, Q_A, by strong illumination inhibits the electron transfer through Q_A, which leads to charge recombination and hence to the formation of triplet state chlorophyll (Chl). The triplet Chl reacts with oxygen to form singlet oxygen, which is highly reactive and causes the destruction of P680. In the presence of oxygen, the degradation of D1 proteins is also induced, and the repair cycle of PSII starts. Secondly, when the activity of the donor side of PSII is somehow insufficient to reduce $P680^+$, the strong oxidizing radicals accumulates on the donor side. This donor side photoinhibition also leads to the inactivation of electron transfer and to protein damage [2].

Recently, a selective photoinhibition of photosystem I (PSI) in light-chilled cucumber leaves was reported by Terashima *et al.* [3]. At least in cucumber leaves, the damage to PSI occurs when leaves are chilled at weak light (<100 μmol m^{-2} s^{-1}), while the damage to PSII is induced when they are chilled at strong light (>500 μmol m^{-2} s^{-1}) [4]. The low temperature photoinhibition of PSI is initiated by the inactivation of the acceptor side and the destruction of the *psa*B gene product, a major subunit of the PSI reaction center [5].

As mentioned so far, there have been many reports on the lesion sites of low temperature photoinhibition in the photosynthetic apparatus of cucumber, in comparison with the sites in other plant species of different chilling sensitivities. However, few are reported on the differences among cucumber cultivars.

For the comparison of chilling sensitivities among cultivars of cucumber, all known defense mechanisms in chilling resistant plants should be considered, although some are not well-developed in cucumber. Therefore, in this study, three cucumber cultivars were selected based on the preliminary experiments in the lab and the field test on their growth under chilling stress, and their sensitivities to chilling stress in the light were compared using several non-destructive techniques that measure

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various activities of photosynthetic apparatus.

MATERIALS AND METHODS

Plant materials and chilling treatment

Seeds of cucumber (*Cucumis sativus* L.) cultivars donated from National Pusan Horticultural Experiment Station were grown in a growth chamber under continuous light with PFD of 100 μmol m^{-2} s^{-1} provided by white fluorescent lamps. Names of the cultivars are Gahachungjang, Banbaekjijeo and Gaeryangsymji, and the abbreviated names we used in this report are GH, BB and GR, respectively. Leaf discs excised from fully expanded young leaves were floated on water with the abaxial side down. For the light-chilling treatment, the leaf discs were illuminated on their adaxial side at 4°C under the same light condition that used for their growth.

Measurement of quantum yields of PSII photochemistry

For the measurement of Fv/Fm, the potential quantum yield of photochemical reactions in PSII or photochemical efficiency in short, a portable Plant Efficiency Analyzer (PEA, Hansatech, England) was used as described in Eu *et al.* [6]. Before the measurement, leaf discs were dark-adapted for 10 min at 25°C. The maximum variable fluorescence (Fv) was obtained by subtraction of the initial Chl fluorescence (Fo) from the maximum yield of fluorescence (Fm).

For the measurement of quantum yield of PSII electron transport under light-stress conditions, Chl fluorescence was measured using a pulse-amplitude modulated fluorometer (PAM-2000, Walz, Germany). The quantum yield of electron transport at photosystem II (PSII), Φ_{PSII}, were determined as described in Genty *et al.* [7].

Measurement of Chl fluorescence quenching during light-chilling

For Chl fluorescence quenching parameters, Chl fluorescence was measured using a pulse-amplitude modulated fluorometer (PAM-2000, Walz, Germany). The qP and non-photochemical quenching (NPQ) parameters were calculated by the equations described in Kooten and Snel [8].

$$qP=(Fm'-Ft)/(Fm'-Fo'), \text{ and } NPQ=(Fm-Fm')/Fm'$$

where Fo' was measured after switching off the actinic light and simultaneously applying 3 s of far red light (735 nm) at 4°C, and Fm' is maximum yield of fluorescence in light-acclimated leaves. Ft is the steady-state fluorescence level under the continuous actinic illumination. In this experiment, qP was measured at 4°C. Fm was measured after 10 min dark-adaptation at room temperature prior to chilling.

Measurement of Chl fluorescence induction transients after light-chilling

Chl fluorescence transients from the adaxial side of the leaves were measured using PAM-2000 (Walz, Germany) as described by Ha *et al.* [9]. Chl fluorescence transients were measured after dark-adaptation of light-chilled leaves for 10 min. Leaves were dark-adapted either at 4°C or at room temperature. Fo was measured with modulating beam (0.2 μmol m^{-2} s^{-1}), and actinic light (150 μmol m^{-2} s^{-1}) was provided by a halogen lamp. Fm was induced by a saturated light pulse (3200 μmol m^{-2} s^{-1}) provided by a halogen lamp for 0.8 s per 30 s.

The photochemical quenching (qQ) and the non-photochemical quenching (qN) were measured at the steady state with the actinic light (A.L.) turned on. The energy-dependent quenching (qE) was measured after the A.L. was turned off. Quenching coefficients were calculated as described by Oxoborough and Horton [10];

$$qQ=1-Ft/Fm', \; qN=1-Fm'/Fv, \text{ and } qE=1-Fm'/Fm'_E,$$

where Fm'_E is Fm' measured after the qE relaxation reached to a plateau with the A.L turned off.

The fast relaxing component of NPQ (qf) is considered to be equivalent to qE, that is defined as $(Fm/Fm')-(Fm/Fm^R)$, where Fm^R is the maximum fluorescence for qf [11]. Fm^R can be calculated after subtracting the maximum fluorescence for slow relaxing component of NPQ from Fm. However, we took the maximum fluorescence measured after dark-relaxation for 2 min as Fm^R, because Fm' became greater than Fm (measured after light-chilling) during recovery at room temperature.

Measurement of oxidizable P700 content

The content of oxidizable P700 ($[P700^+]$) was monitored with a Pulse-Amplitude-Modulation (PAM) chlorophyll fluorometer (Walz, Germany) in the reflectance mode equipped with dual wavelength emitter, a sample (810 nm, 30 nm HBW) and a reference (860 nm, 40 nm HBW) light pulse, respectively [12]. Far-red (FR) light (λ_{max}=745 nm) was provided by the 102-FR light source (Walz, Germany). The light intensity was strong enough to saturate control leaves, and the same saturating light was used for the chilled leaves, although it was not saturating. Leaf discs were illuminated with FR light for about 20 to 30 s until a steady P700 oxidation state was reached. The amplitude of $P700^+$ absorbance in the form of ΔA810/860, a differential absorbance change (810 nm minus 860 nm), was measured at 25°C after 10 min dark adaptation and expressed as relative values.

RESULTS

Chl fluorescence parameter Fv/Fm during chilling in the light

The photoinhibitory damage to PSII is frequently monitored by the decrease of photochemical efficiency or Fv/Fm. As shown in Figure 1, the cultivar GH was the most tolerant to chilling stress for 6 h in the light, and GR was the least tolerant among the three cucumber cultivars. This is in agreement with the previous result of field test on the overall growth patterns of cucumber cultivars during a winter season in 1999 made by the National Pusan Horticultural Experiment

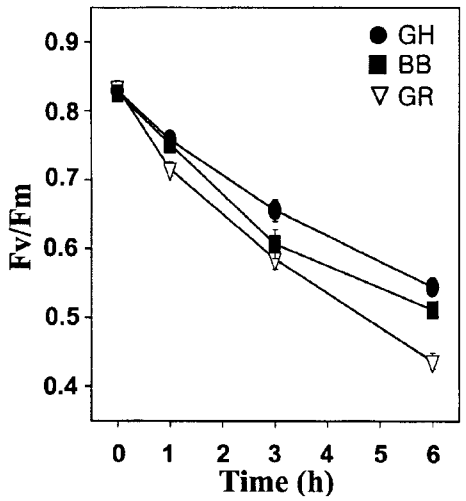

Figure 1. The effect of light-chilling on the photochemical efficiency of PSII (Fv/Fm) in the three cucumber cultivars. The leaf discs were chilled at 4°C under an irradiance of 100 μmol m^{-2} s^{-1} and were dark-adapted for 10 min at 25°C before measurements. The three cucumber cultivars are Gahachungjang (●, GH), Banbaekjijeo (■, BB) and Gaeryangsymji (▽, GR). Error bars indicate SE (n=6).

Station (Korea) (H. T. Kim, personal communication). The Fv/Fm values for un-chilled control leaves were about 0.82 during the whole period of illumination.

Oxidizable P700 content during chilling in the light

The light intensity applied during chilling was 100 μmol m^{-2} s^{-1}, which was the same as that used for the growth of plants. Under this condition, we can expect photoinhibitory damages to PSI as well as damages to PSII. As shown in Figure 2, the oxidizable content of P700 decreased gradually during light-chilling for 6 h. After light-chilling for 6 h, the content remained in GH was significantly higher than the contents in the other two cultivars.

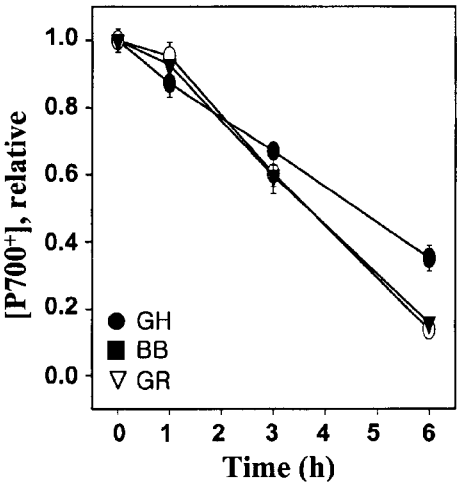

Figure 2. The effect of light-chilling on the photooxidizable P700 content ([$P700^+$]) in the three cucumber cultivars. The leaf discs were chilled at 4°C under an irradiance of 100 μmol m^{-2} s^{-1} and were dark-adapted for 10 min at 25°C before measurements. Full names of the abbreviated cultivars are shown in Figure 1. Error bars indicate SE (n=3).

Quantum yield of PSII during chilling in the light

The quantum yield of PSII photochemistry, Φ_{PSII}, measures the proportion of the light absorbed by Chl associated with PSII that is used in photochemistry [13]. This parameter measures the actual yield of PSII in light-chilling acclimated leaves in contrast to Fv/Fm that measures the maximum yield of PSII after dark-adaptation for 10 min.

As shown in Figure 3, Φ_{PSII} declined markedly in all the three cultivars during the first 3 h of light-chilling, and the values became almost zero after light-chilling for 6 h. The rate of Φ_{PSII} decrease in GH was relatively slower compared with the other two cultivars, and the value after light-chilling for 6 h was about 10% of the value in un-chilled control leaves. Φ_{PSII} at 0 h was measured at room temperature under the same light condition that used during light-chilling.

Photochemical quenching (1-qP) during chilling in the light

By measuring the parameter 1−qP, we can estimate the fraction of reduced primary electron acceptor of PSII, Q_A or the proportion of PSII reaction centers that are closed [13]. During light-chilling, 1−qP increased rapidly in all the three cultivars during the first 3 h, and the values became near 1 after light-chilling for 6 h (Figure 4). The curves in Figure 4 are very close to the mirror images of the curves shown in Figure 3. The rate of 1−qP increase in GH was relatively

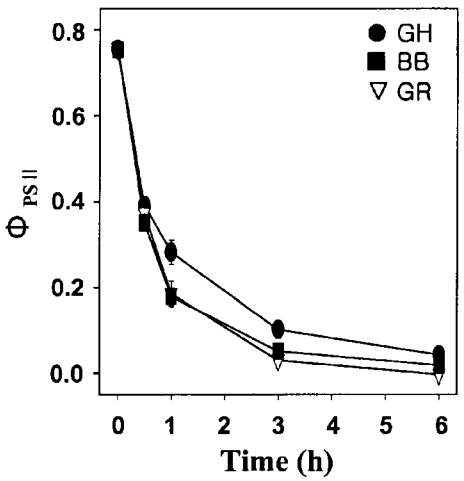

Figure 3. The effect of light-chilling on the quantum yield of PSII (Φ_{PSII}) in the three cucumber cultivars. The leaf discs were chilled at 4°C under an irradiance 100 μmol m^{-2} s^{-1}. Φ_{PSII} was measured while leaf discs were chilled in the light. Full names of the abbreviated cultivars are shown in Figure 1. Error bars indicate SE (n=5).

slower compared with the other two cultivars, and the value after light-chilling for 6 h was about 0.83. The values reached

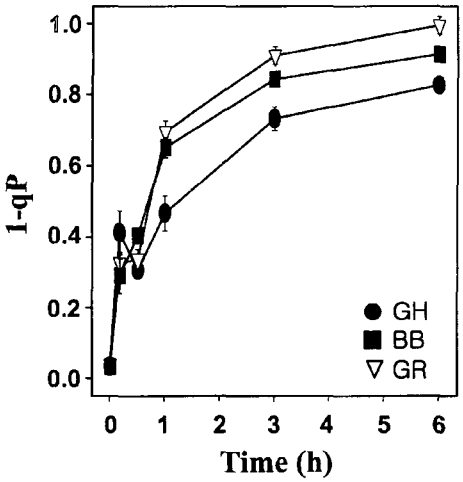

Figure 4. The effect of light-chilling on the reduced state of Q_A (1-qP) in the three cucumber cultivars. The leaf discs were chilled at 4 °C under an irradiance 100 μmol $m^{-2}s^{-1}$. The 1-qP was measured while leaf discs were chilled in the light. Full names of the abbreviated cultivars are shown in Figure 1. Error bars indicate SE (n=5).

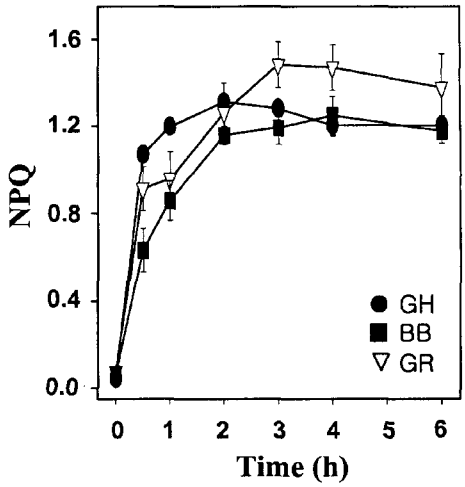

Figure 5. Time courses of the development of non-photochemical fluorescence quenching (NPQ) during light-chilling in the three cucumber cultivars. The leaf discs were chilled at 4°C in an irradiance 100 μmol $m^{-2}s^{-1}$. The NPQ was measured while leaf discs were chilled in the light. Fm' at zero time of chilling was measured after keeping the discs in the light for 30 min at room temperature, and Fm was measured after dark-adaptation for 10 min before the onset of chilling. Full names of the abbreviated cultivars are shown in Figure 1. Error bars indicate SE (n=6).

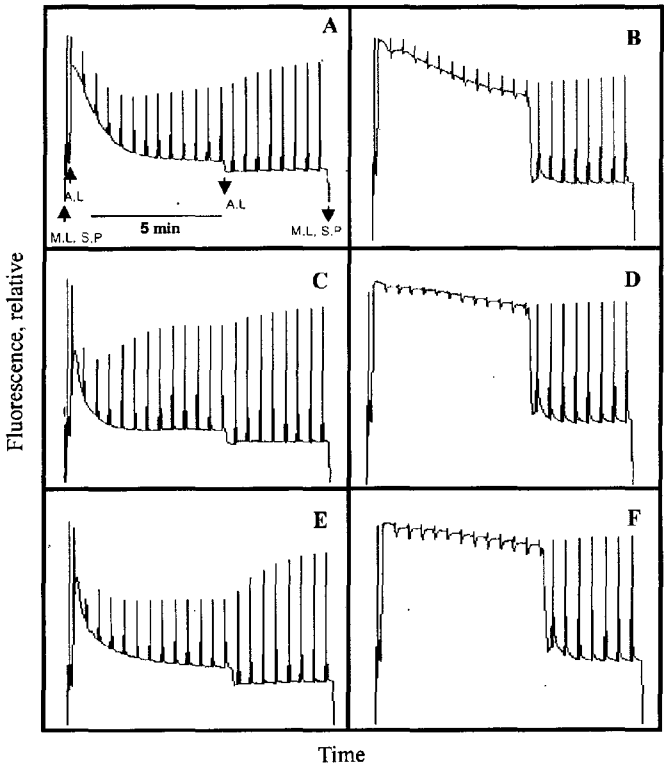

Figure 6. Effects of chilling at in the light on the fluorescence induction transients of three cucumber cultivars. Name of the cultivar for A and B is Gahachungjang (GH), for C and D is Banbaekjijeo (BB) and for E and F is Gaeryangsymji (GR). A, C and E are transients from untreated leaf discs before chilling, and B, D and F are transients from leaf discs after chilling at 4°C in an irradiance 100 μmol $m^{-2}s^{-1}$ for 1 h. After chilling, leaf discs were kept in darkness at 4°C for 10 min before the illumination of saturating pulse for measurements of Fm. The transients were recorded at 4°C. Control and chilled leaf discs in a cultivar were taken from a single leaf. Upward arrows indicate the onset of illumination by the measuring light (M.L), saturating pulse (S.P) and actinic light (A.L) and downward arrows indicate the termination of M.L, S.P and A.L illumination. After A.L (150 μmol m^{-2} s^{-1}) was turned on, S.Ps (3200 μmol m^{-2} s^{-1}) were applied in every 30 s.

after light-chilling for 6 h was 0.91 for BB, and 1.00 for GR, respectively.

Non-photochemical quenching (NPQ) during chilling in the light

The increase in the extent of dissipation of excess light energy as heat was monitored by means of NPQ developing during light-chilling (Figure 5). For the calculation of NPQ, Fm was measured just before the onset of light-chilling at room temperature after a dark-adaptation period for 10 min. The NPQ development was saturated more rapidly (within 2 h) in GH than in the other two cultivars (within 3~4 h). In GH, NPQ developed very rapidly reaching more than 80% of the saturated value after 30 min of light-chilling.

Chl fluorescence induction kinetics at 4°C after light-chilling

Physiological states of leaves after light-chilling were monitored by measuring Chl fluorescence induction kinetics or by quenching analysis. When exposed to actinic light at room temperature, un-chilled leaves showed typical Kautsky transients as shown in Figures 6A, 6C and 6E. However, when the fluorescence induction transients were measured again at 4°C after light-chilling for 1 h and dark-adaptation for 10 min at 4°C, both non-photochemical (qN) and photochemical quenching (qQ) were not developed with relatively high variable fluorescence in GR and BB (Figures 6D and 6F). In GH, both non-photochemical and photochemical quenching were developed relatively well by the illumination of actinic light at 4°C, but energy-dependent quenching (qE) was not observed (Figure 6B). As shown in Table 1, these quenching coefficients are calculated from the fluorescence induction curves plotted from 3 independent experiments (Curves in Figure 6 are typical ones). After light-chilling for 1 h, qQ and qN in GH was almost two times greater than the values in the other two cultivars.

Table 1. Changes in fluorescence quenching coefficients obtained from fluorescence induction transients before and after light-chilling of leaf discs of three cucumber cultivars. The quenching coefficients were calculated from transients plotted from 3 independent experiments (Curves in Figure 6 are typical ones), and the values inside the parentheses are SE (n=3). Full names of the abbreviated cultivars are shown in Figure 1

	Before chilling			After chilling for 1 h		
	qQ	qN	qE	qQ	qN	qE
GH	0.67 (0.01)	0.30 (0.05)	0.08 (0.03)	0.07 (0.00)	0.38 (0.01)	0.01 (0.00)
BB	0.65 (0.00)	0.33 (0.02)	0.1 (0.01)	0.04 (0.00)	0.21 (0.01)	0.00 (0.00)
GR	0.57 (0.02)	0.43 (0.08)	0.18 (0.04)	0.04 (0.00)	0.26 (0.02)	0.02 (0.01)

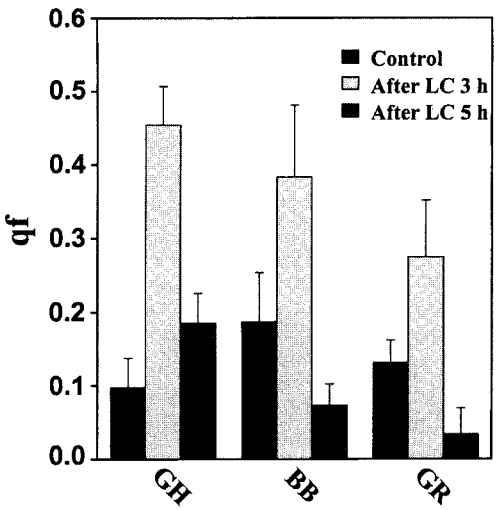

Figure 7. Changes in the fast relaxing component of NPQ (qf) after light-chilling for 3 and 5 h in the three cucumber cultivars. The leaf discs were chilled at 4°C in an irradiance 100 μmol m^{-2} s^{-1}. After chilling, leaf discs were kept in darkness at room temperature for 10 min before the illumination of saturating pulse for measurements of Fm. The transients were also recorded at room temperature. Fm' values used for the calculation of qf were measured just after A.L off and once more after relaxing the leaf discs in darkness for 2 min. Full names of the abbreviated cultivars are shown in Figure 1. Error bars indicated SE (n=3).

Chl fluorescence induction kinetics at room temperature after light-chilling

When the Kautsky transients were measured at room temperature, these differences among cultivars were not observed (data not shown), indicating that the changes shown in Figure 6 and Table 1 are reversible.

However, when transients were measured after light-chilling for more than 3 h, the capacity for qE seemed to be hindered in BB and GR (data not shown). After non-photochemical quenching was induced by illumination of actinic light at 25°C, and its fast relaxing component (qf) was measured after dark-adaptation for 2 min. Because qE part of NPQ is thought to be relaxed within 2 min, qf can be considered to be equivalent to qE or the capacity of proton gradient formation. As shown in Figure 7, qf increased by light-chilling in all the three cultivars, more rapidly in GH than in GR and BB. Although qf values decreased by prolonged chilling in all the three cultivars, the changes were more pronounced in GR and BB.

DISCUSSION

Cucumber is known to be a chilling-sensitive plant and therefore its lesion sites in photosynthetic apparatus have been usually studied comparing with other chilling-tolerant plant species. In the present study, we could find substantial differences in the susceptibility to chilling-induced photoinhibition both

in the activity of PSII as described below and in the activity of PSI measured as changes in the content of oxidizable P700 (Figure 2) among three cucumber cultivars. In all the parameters tested, GH was shown to be more tolerant to chilling stress in the light than the other two cultivars.

The decrease of Fv/Fm in the light is often ascribed to the photoinhibitory damage in PSII reaction centers [14,15], and the damage to the PSII reaction center leads to a decline in the quantum yield of photosynthesis, Φ_{PSII} [16]. However, the initial decrease of Fv/Fm during light-chilling is partly due to the down-regulation or photoinactivation of PSII through an increase in the non-radiative energy dissipation [17]. The down-regulation mechanism has been correlated with the trans-thylakoidal proton gradient formation and the epoxidation of zeaxanthin via the xanthophylls cycle [18,19] and also with the phosphorylation of thylakoid phosphoproteins [20].

During light-chilling, Φ_{PSII} declined more rapidly (Figure 3) than Fv/Fm in all the three cultivars. This result indicates that significantly inactivated PSII reaction centers can be reactivated, because Fv/Fm is measured after dark-adaptation for 10 min at room temperature, but Φ_{PSII} is measured in leaves under light-chilling stress. This rapid reactivation processes include the relaxation of trans-thylakoid proton gradient. However, this period is relatively short for the epoxidation of zeaxanthin [17] and for the dephosphorylation of thylakoid phosphoproteins. The half-life for LHCII dephosphorylation in darkness is approximately 10~20 min [21], but the process became much slower after chilling in the light (data not shown). Therefore, the decrease of Fv/Fm during light-chilling is not totally due to the irreversible damage in PSII. To examine the extent of irreversible damage, the decrease of Fv/Fm should be measured after a dark-adaptation period for more than 24 h.

After chilling for more than 3 h, the cultivar GH could still retain some PSII quantum yield (Figure 3), indicating that some electrons could flow around PSII, because the relative PSII-driven electron transport rate can be calculated as $\Phi_{PSII} \times 0.5 \times$ PFD $\times$ leaf absorptance (0.85) according to Genty *et al.* [7]. If the electron transport chain around PSII is blocked, Q_A become reduced and the parameter 1−qP shows the fraction of reduced Q_A. As shown in Figure 4, the values in the two cultivars other than GH became close to 1 after light-chilling for 3 h.

The extent of photoinhibition is closely correlated with the reduction state of Q_A under environmental stress [22, 23], and PSII reaction centers with fully reduced primary quinone acceptors (Q_A^-) are highly susceptible to photoinhibition and potential photodamage [24]. Therefore, the fast reduction of Q_A under chilling stress can be an important reason for the chilling sensitivity in BB and GR observed in this study. On the other hand, in GH, Q_A was not fully reduced during light-chilling for 6 h, and the possible electron carriers in GH, that is active at low temperature, are under investigation.

NPQ mechanism is an important protective response which could dissipate excitation energy in light-harvesting antenna systems, thus preventing over-reduction of Q_A [24,25]. The amplitude of developed NPQ after light-chilling was 1.2~1.4 in cucumber (Figure 5), and it is relatively small compared with the value observed in barley and rice (2.4~3) [26]. Although they are small, we could observe differences in the NPQ development kinetics among the three cucumber cultivars.

During chilling in the light, the development of NPQ shown in Figure 5 is also matched with the increase in 1−qP (Figure 4) or with the decrease in Φ_{PSII} (Figure 3). We expect the turnover rates of dark reactions are even more restricted than photosynthetic electron transport, which results in an accumulation of energy-rich compounds (ATP and NADPH), resulting in the accumulation of protons in the thylakoid lumen, as seen by the rapid development of NPQ (Figure 5). This may lead to feedback limitation of electron transport and contribute to the increase in 1−qP (Figure 4) and the decrease in the rate of electron transport (data not shown).

Photoinactivation of PSII is often correlated with the development of NPQ. An NPQ component that developed rapidly is induced in the presence of a high pH gradient across the thylakoid membrane and is called ΔpH-dependent quenching, and we expect this component relaxes fast, too. In this experiment, the energy-dependent quenching coefficient (qE) became vanished when the Kautsky transients were monitored at 4°C after light-chilling for 1 h, and qE became measurable again when the transients were recorded at room temperature (data not shown), indicating that the disappearance of qE is reversible.

The fast relaxing component of NPQ (qf) can be considered to be equivalent to qE. In this study, we measured qf after dark-adaptation for 2 min, assuming that 2 min is long enough for the completion of the relaxation of qf. After room temperature photoinhibition, qf relaxes *in vivo* within 30 s, and the next slow component relaxes in about 10 min [27]. In GH, the relative contribution of qf to NPQ is greater than those in the other two cultivars (Figure 7), and the difference is matched in the faster development of NPQ (Figure 5).

When the Kautsky transients were recorded at room temperature after light-chilling for 5 h, qf decreased significantly compared with the value after light-chilling for 3 h. As Terashima *et al.* [28] also reported the suppression of non-photochemical quenching after chilling cucumber leaves in the light for 5 h, the decrease in qf is due to the hindrance of pH formation across the thylakoid membrane by uncoupling ATPase. Therefore, the disappearance of qE observed in Figure 6 and Table 1 is due to the ATPase uncoupled during the first light-chilling for 1 h. As mentioned earlier, ATPase seems to be recoupled during the dark-adaptation period at room temperature. Terashima *et al.* [28] also reported recoupling of the thylakoids by rewarming of the chilled cucumber leaves. However, the small fraction of qf shown in BB and GR after light-chilling for 5 h (Figure 7) may also indicates that significant fraction of PSII centers are irreversibly damaged after light-chilling for 5 h.

To conclude, the susceptibility of three cultivars of cucumber against chilling-induced photoinhibition is less in GH than in BB and GR in most of the parameters measuring activities of PSI and PSII. In GH, (1) some electrons can flow around PSII at chilling temperature keeping Φ_{PSII} higher than those in BB and GR, (2) the defense mechanisms with reversible photoinactivation of PSII activity are relatively well-developed as shown by the rapid NPQ development and high quenching coefficients. In contrast, photosynthetic apparatus in BB and GR are supposed to be irreversibly damaged more easily than in GH.

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Abbreviations – Chl, Chlorophyll; Fm', maximum yield of fluorescence in light-acclimated leaves; Fm, maximal fluorescence; Fo, minimal or initial fluorescence; Fv, variable fluorescence; NPQ, non-photochemical quenching in light-acclimated leaves; PS, photosystem; qE, energy-dependent quenching from the analysis of Chl fluorescence transients; qf, fast relaxing component of NPQ; qN, non-photochemical quenching from the analysis of Chl fluorescence transients; qP, photochemical quenching in light-acclimated leaves; qQ, photochemical quenching from the analysis of Chl fluorescence transients; Φ_{PSII} quantum yield of PS II under stressed condition.

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